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VISUAL PATTERN PERCEPTION FOLLOWING SUBPIAL SLICING AND TANTALUM WIRE IMPLANTATIONS IN THE VISUAL CORTEX[1]

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Important integrative roles have been ascribed in theory to the tangential intragriseal irradiation across the cerebral cortex of excitatory effects in the form of discrete nerve impulses and mass direct currents. In an earlier effort to test the possible importance of tangential intracortical conduction, we found that multiple subpial knife cuts extending through the depth of the gray matter and placed in criss-cross patterns throughout the sensorimotor and neighboring cortex of the monkey failed to produce any marked disruption of motor coordination (10). Similar subpial slicing of the exposed striate cortex in the monkey likewise failed to cause any detectable impairment of function in simple tests of visual perception. The performance of control cases with the same cortical area excised proved to be sufficiently good, however, to render this latter finding indecisive. Visual perception in the monkey has been found to survive also an electrical short-circuiting of the exposed portion of the striate cortex with overlaid gold bands and inserted pins (5).

No significant functional role of transcortical conduction either of nerve impulses or of gross direct current has been revealed in the foregoing. However, a final interpretation cannot be reached in the absence of further surgical controls along with more refined functional tests. Definitive experiments with respect to vision in particular are needed because many of our current concepts of cerebral organization are based specifically on phenomena of visual perception (2, 3, 4, 7, 8, 11). Moreover, hypotheses concerning the cerebral mechanisms of visual pattern perception constitute at the present time the most specific formulations available for the neural correlates of subjective experience.

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METHOD

Apparatus, Subjects, and General Procedure

Cats, one-half to three-fourths grown at the start, were trained to select an equilateral triangle when paired with various ones of the series of other imperfect triangular patterns of the same dimensions shown in Figure 1. A darkened discrimination box was designed in which the two stimulus figures were presented side by side, 10 cm. apart in two doors at one end of the box. The white translucent stimulus figures illuminated by transmitted light from an outside source stood out distinctly in the dark uncomplicated by frame or border relations. The outer edges of the positive equilateral triangle were 7.5 cm. in length, and the animals made their choice at distances ranging from approximately 10 to 35 cm. By selecting and pushing open the correct door holding the positive figure the cats obtained a morsel of food. A sliding bolt prevented the incorrect door from opening more than 1 cm. When an incorrect

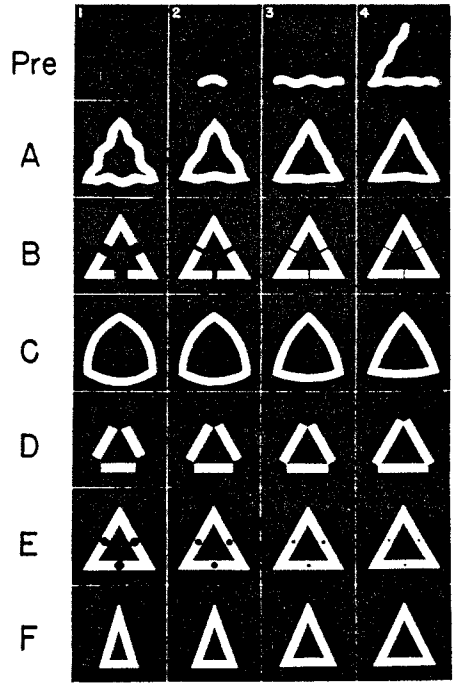

FIG. 1. Test scale of negative figures that were paired individually with the single positive figure which was an equilateral triangle like E4 without the dots (see also Fig. 3A). Training proceeded from left to right, top to bottom, beginning with the preliminary series, *Pre*.

choice was made, the cats failed to get food and received mild punishment in the form of abrupt withdrawal from the box, rough handling, and an occasional light slap.

In order to test specifically for possible pattern-disturbing effects of the surgical procedures, the negative stimulus figures were designed in the form of distortions or imperfections of the positive figure. For each pattern type four figures of increasing difficulty were arbitrarily selected to form the 6 series, A to F, of the test scale shown in Figure 1. More difficult discriminations than those of column 4 were possible, but the extra time involved in training and the instability of the more liminal discriminations contraindicated their use for postoperative testing.

Training Program

The regular training schedule involved 20 to 30 trials per day, five to six days per week. Irregularities were common, however, owing particularly to suspension of training while the cats had respiratory and other infections and during interruptions for other experiments. As we were not concerned directly with the learning process or memory capacity as such, considerable individual variation was permitted in the training program.

The cats were trained to a criterion of 17 correct out of 20 consecutive trials on all the negative figures with which they were to be tested after surgery. Approximately 50 training days were required on the average to master the complete series A through F. Surgery was postponed until at least 50, and generally many more, overtraining trials had been run on each of the top figures. During the overtraining period and in all the postoperative tests, the figures were interchanged at random in accordance with Gellerman's (1) principles. Care was also taken during these trials to eliminate the use of accessory cues based on brightness, total flux of light, odor, sound, or on accidental characteristics of individual stimulus cards or of individual trainers.

Operative Procedure

The operations were performed aseptically with the cats under sodium pentobarbital anesthesia (38 mg. per 1 kg. body weight, intraperitoneal). The skull was opened widely on each side and across the midline. The cortical knife cuts were made with subpial knives (10) with cutting blades of 1.9 and 2.1 mm. in depth. The metallic wires inserted in the cortex were cut from surgical sutures of tantalum, B and S gauge No. 30 and No. 33. Tantalum, with an electrical conductivity approximately one-seventh that of copper, was chosen because of its extreme biological inertness. No effort was made to confine the wires to the cortical gray and many of them extended deep into or through the subjacent white matter. Visual cortex both I and II as described by Talbot and Marshall (12) were included in all cases. Excision of the superior colliculi was started with a shallow subpial knife, after which the loose tissue was removed with weak suction. Preliminary removal of the visual cortex on one side or, in other cases (*Mrc* and *Stf*), division of the caudal third of the corpus callosum was involved in removal of the colliculi. The finer aspects of all operations were carried out with the aid of a wide field stereoscopic microscope with a magnification of 7×. A medial bridge of bone 1 to 2 cm. wide was replaced over the sagittal sinus. Procaine penicillin G (300,000 units) was injected intramuscularly at the beginning of the operation and again on each of the next three days.

A minimum of ten days was usually allowed for recovery from the surgery. The top test patterns were then introduced with a preliminary trial on each of the simpler stimulus cards of the same pattern type. If the animal failed to make criterion it was tested on the next easier figure of the series. As a rule, only one negative series was tested on a given day. However, the foregoing general procedure was evolved gradually in the course of the experiments, and exceptions were common especially among the earlier cases.

Finally, following a lethal dose of sodium pentobarbital, the head was perfused post mortem with 10% formalin, and the brain removed. Appropriate records were then made in the form of X rays, photographs, and camera-lucida drawings. The lesions were studied histologically in sections prepared with the Weil myelin, Mallory connective tissue, and cresyl violet Nissl stains.

CASE RECORDS

Subpial Slicing

Case Snt. Left and right superior colliculi and the left visual cortex were removed prior to training. *Snt* was then taught to discriminate between the positive equilateral triangle and the negative figures A3, B3, C3, D4, and E3, in a total of 48 days spread over a period of four and one-half months. This included only 50–70 overtraining trials per figure, and the performance remained comparatively erratic. The remaining (right) visual cortex was thereupon sliced with intersecting knife cuts as illustrated in Figure 2.

The postoperative tests were delayed in this first case by development under the incision of an abscess which drained during the second week after operation and gradually closed during the third. Scores on the postoperative tests conducted over a ten-day period beginning on the 18th day after operation were somewhat below the preoperative level at the beginning on the A3 and B3 figures but by the 28th day, *Snt* had achieved criterion or better on all his top test figures.

On post-mortem examination the knife cuts in the right cortex were found extending through the gray matter in most places and at erratic intervals a short distance into the white matter (cf. Fig. 4). The superior colliculus was

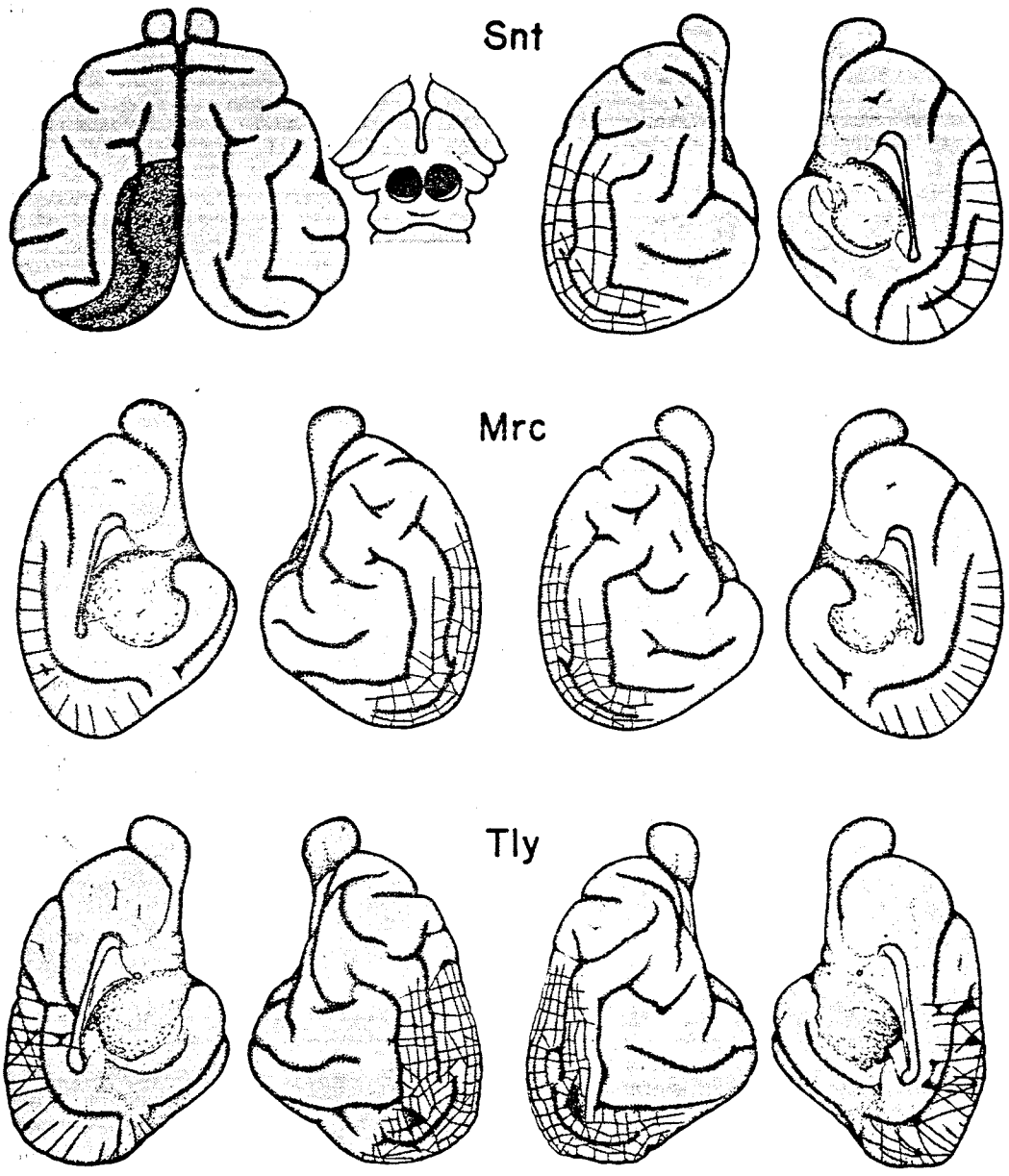

FIG. 2. Camera-lucida tracings showing preliminary lesions in case *Snt*, and medial and lateral views of the patterns of subpial knife cuts in cases *Snt*, *Mrc*, and *Tly*.

missing on the left side except for a small lip at the posterior edge. On the right, the latero-caudal border of the colliculus was intact, but it appeared doubtful that any optic fibers to this area had escaped the lesion.

Case Mrc. This cat was trained to discriminate figures A3, B4, C4, D4, E3, and F3 with 90 to 160 overtraining trials for each figure. The preoperative training required 76 days spread over a period of six months. The visual cortex in both hemispheres was then sliced with multiple subpial knife cuts in the patterns shown in Figure 2.

Beginning on day 11 after operation, *Mrc*

ran the first 20 trials on each of the figures A3, C4, D4, and F3 with no errors. Perfect scores were also obtained by day 20 on B4 and E3, but not without a significant number of initial errors (11 and 14 respectively) suggesting some selective effect of the cortical lesions for the B and E patterns.

A second operation six weeks after the first was undertaken to remove the superior colliculi. There was no evidence of vision during the first several days after this operation. Some visual capacity had returned by the end of the second week and testing was resumed. One month after the second operation the highest figures on which criterion had been attained were A2, B2, C1, E1, D4, and F1. The pupils remained widely dilated after the second operation indicating damage to the pretectal nuclei (6). Impairment of the mechanisms for focusing may thus have been a complicating factor. Discrimination even at these lower levels of the test scale, however, indicates a fair capacity for form discrimination comparable at least to that involved in differentiating, for example, a triangle from a circle.

The midbrain lesions invaded the deeper layers of the colliculi as far as the stratum griseum profundum and extended far forward on both sides into the pretectal nuclei. In addition an area of secondary degeneration on the left side extended ventrally into the tegmentum to the level of the aquaduct. On the left side the optic layers of the colliculus were missing completely. On the right side the posterior and posterolateral margins, totaling approximately one-fifth the surface area, were intact as was the lateral edge of the brachium. In the cortex the knife-cut scars were similar in appearance to those in *Snt* and *Tly* (cf. Fig. 4).

Case Tly. Having obtained only a minor lowering of performance level from the preceding patterns of knife cuts, we decided next to carry the subpial slicing to an extreme. *Tly* was trained to figures A4, B4, C4, D4, E4, and F4 with 290–510 overtraining trials per figure in a total of 153 days spread over a period of ten months. The visual cortex was then sliced bilaterally as shown in Figure 2.

During the first four days after operation *Tly* seemed completely blind. Signs of returning vision were noticed on the fifth day and became rapidly more pronounced during the second week. His postoperative performance is summarized in Table 1. By the 31st day after operation he managed to attain the criterion of 17 correct out of 20 on all his top figures except for the B and E series on which he fell to the third and second levels respectively.

Because his vision seemed to be improving further, *Tly* was retained for later testing after other phases of the experiment had been completed. Meantime in preparation for further studies the training box was remodeled with improvements that raised the normal discrimination levels a little higher than those of the original box. The discriminations which *Tly* was able to achieve on the new box during the following three months are shown in Figure 3A. Judging from the performance of two unoperated cats in the same box, the records of *Tly* would seem to be within, or very close to, the normal range for top capacity in this apparatus.

A new positive triangle and new negative figures A3 and C3 were constructed at one-half the standard dimensions. When tested on these new half-size figures, *Tly* transferred at once with only a few extra errors at the beginning indicating a high degree of equivalence in the two sets of figures. Seventeen correct out of 20 consecutive trials was attained in a total of 22 and 23 trials on the A and C figures respectively. When *Tly* was confronted with two entirely new kinds of patterns at the same reduced dimensions (a square and a circle, each 10.2 mm.^{2} in area, with the circle positive), it

TABLE 1

Postoperative Performance of *Tly*

Days after operation	12			13			15			16	17			19			26	27	28	30				31			32	33	37
Negative figures	B4	B3	B2	C4	C3	C2	F4	F3	F2	D4	E4	E3	E2	A4	A3	A2	B3	B4	B4	C3	C4	F3	F3	F4	F4	A3	A4	A4	B4	E3	D4
Errors	6	8	0	7	5	3	5	5	1	3	4	4	3	4	4	1	8	4	9	2	3	4	1	3	2	2	2	3	13	16	2
Total trials	13	13	20	20	16	20	15	20	20	20	8	9	20	7	16	20	50	15	28	20	20	9	20	10	20	20	3	20	40	43	20

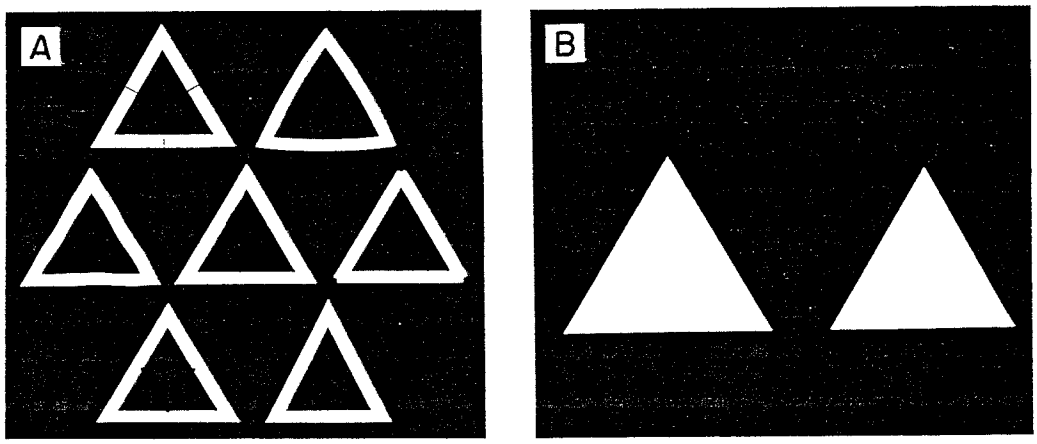

FIG. 3A. Six most difficult negative figures discriminated by *Tly* after operation, with the positive equilateral triangle in center. 3B. Size discrimination learned postoperatively by *Tly*. Sides of the larger triangle measured 7.5 cm. Both A and B are from photostats of the original stimulus cards.

required a total of 357 trials in four days before the learning criterion was achieved.

Capacity for size discrimination was then tested on plain equilateral triangles with the larger triangle positive and with light intensity varied independently of size. In the course of 480 trials in five days, *Tly* achieved criterion on the patterns shown in Figure 3B. Finally, *Tly* learned in 61 trials to discriminate vertical vs. horizontal striations, 1.5 cm. in width.

Histological examination of the cortex showed the visual fields to be effectively partitioned as intended. The majority of the scars extended approximately through the depth of the gray matter (Fig. 4). The cuts tended to be shallow at the edges of the fissures but along the center of the convolutions and on the medial surface of the hemispheres they tended to go a short distance into the white matter. In addition to the small areas of complete cortical destruction indicated in black in Figure 2, additional smaller foci of softening and cavitation were found scattered through the visual areas below the surface particularly where the knife cuts intersected or converged (see Fig. 4). The sliced cortex as a whole had undergone considerable shrinkage which is only partially apparent in the photograph. Diffuse and spotty degeneration was discernible in the lateral geniculate nucleus, pars dorsalis, on both sides.

Wire Inserts

Case Jhn. Following the approach of Lashley, Chow, and Semmes (5), we next tried inserting metallic wires into the cortex to distort the normal pattern of direct current. The first case, *Jhn*, was trained to figures A3, B3, C3, D4, and E3 with approximately 40 overtraining trials per figure in a total of 37 days spread over a period of 3 months. Tantalum wires, gauge 33, were then inserted throughout the visual cortex bilaterally as shown in Figure 5.

When *Jhn* was tested on days 10–16 after operation, a level of 17 correct out of 20, or better, was attained immediately on the B, C, and E figures. After two errors in 16 trials on A3, *Jhn* balked and refused to run further, but ran readily the next day 18 correct out of 20 on A3. A second day and a total of 49 trials were required before 17 out of 20 was attained on D4. Because of motivational complications, it is open to question whether the slight trouble on the A and D figures represented any true deficit of perceptual capacity.

Case Jmm. As in *Snt* (cf. Fig. 2) both superior colliculi plus the left visual cortex were removed prior to training. *Jmm* was then trained to the negative figures A3, B2, C3, D2, and E2 in a total of 56 days spread over four months, including approximately 60 overtraining trials per figure. As with case *Snt*,

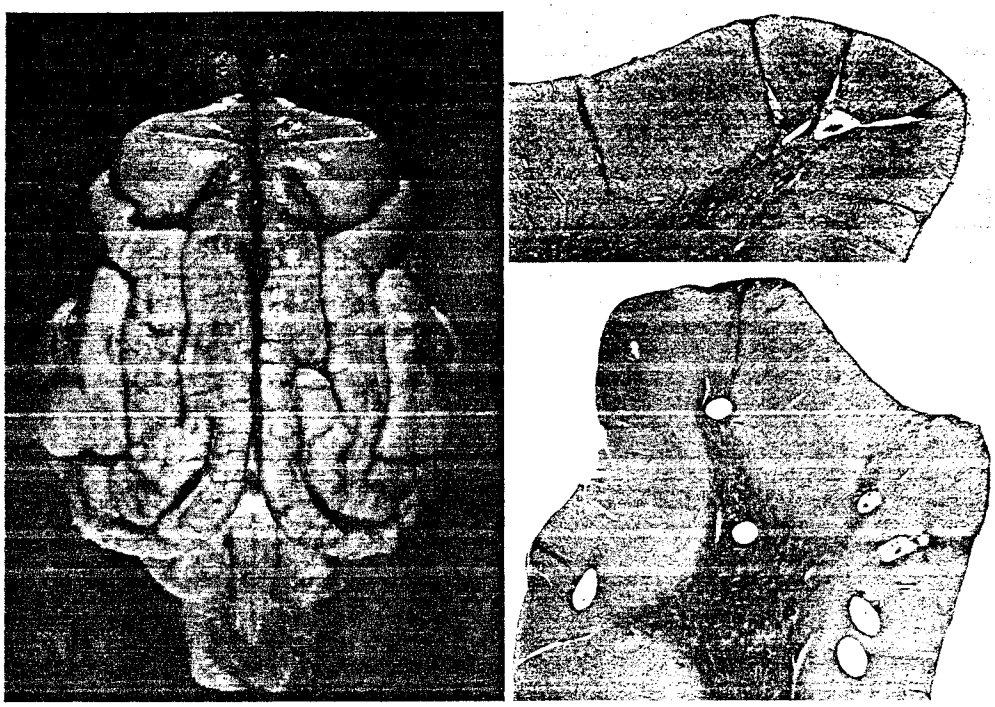

FIG. 4. At left is formalin-fixed brain of *Tly* showing pattern of cortical scars not all of which are visible in the photograph (cf. Fig. 2). At right are photomicrographs of the visual cortex following subpial slicing in *Tly* (top) and after tantalum wire implantation in case *Stf* (below).

learning was below normal in speed and final level of achievement with the cortical and midbrain lesions. Also, the pupils were dilated indicating possible impairment in focusing. The remaining (right) visual cortex was then filled with numerous pins of tantalum wire, gauge 30, much as in *Jhn* shown in Figure 5.

On days 9 to 14 after operation, scores of 18 correct or better were achieved in the first 20 trials on each top test figure. Examination of the brain showed the entire left visual cortex effectively removed and also the optic portion of the left superior colliculus. A thin lateral lip of the superior colliculus remained intact on the right side. The tectal lesions extended on both sides forward into the brachium and pretectal area.

Case Stf. In a total of 61 days spread over a period of four and one-half months *Stf* was trained to figures A3, B4, D4, E3, and F3 including approximately 120 overtraining trials per figure. Tantalum wires, gauge 30, were then inserted throughout the visual cortex of both hemispheres as shown in Figure 5. The postoperative performance is summarized in Table 2. B4 is the only figure on which a criterion score was not achieved on the first attempt. When the negative figures were mixed at random in 94 trials on the last three days, the score was equal to the best of the preoperative records.

Case *Stf* was reoperated upon 44 days after the first operation in an effort to destroy the superior colliculi from a dorsal approach without damaging the visual cortex on either side. As in case *Mrc*, this produced a profound impairment of vision. Recovery was still progressing during the second and third weeks after the operation, and during this period the patterns in columns 1 and 2 of the test scale (see Fig. 1) were the best the cat could discriminate. During the fifth and sixth weeks after the operation, *Stf* again mastered all his top test figures.

On examination of the brain it was found that the anterior two-thirds of the colliculus

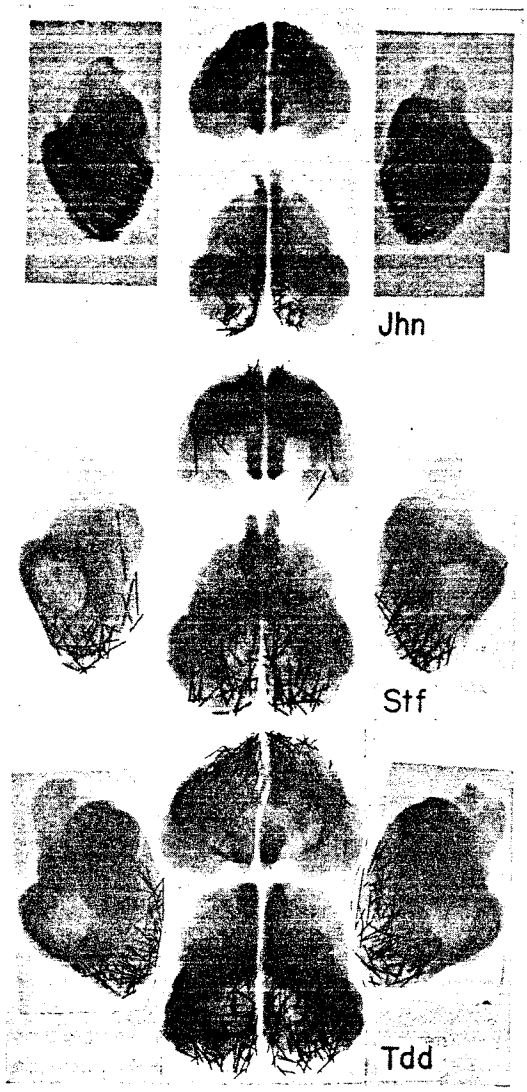

FIG. 5. X-ray pictures of the formalin-fixed cerebral hemispheres of cases *Jhn*, *Stf*, and *Tdd*, taken in three primary planes of the brain to show locations of the implanted wires. Wires tended to migrate in varying degree from their original positions. (Brain of *Jhn* underwent a shrinkage of approximately 17 per cent in linear dimensions as a result of its accidental immersion in alcohol before X rays were taken.)

had been removed on the left side including most of the brachium. The collicular lesions went deep into the stratum medullare profundum with some secondary degeneration anteriorly on the left extending ventral to the posterior commissure. On the right side the posterolateral half of the colliculus remained

TABLE 2
Postoperative Performance of *Stf*

Days after operation	10		11		12	13	14	15	16	17	18	19
Negative figures	A3	B4	B4	B3	D4	C4	E3	F3	B4	MS	MS	MS*
Errors	0	4	4	1	1	0	0	1	3	0	0	3
Total trials	20	7	13	20	20	20	20	20	20	30	30	34

* MS—mixed series in which top negative figures were mixed together and presented in random order.

intact including the lateral half of the brachium. The lesion extended forward through the pretectal nucleus and posteromedial portion of the thalamus to the edge of the pulvinar. The functional impairment caused by the second operation in both *Mrc* and *Stf* may well have been correlated more closely with the effects of pretectal and tegmental damage, transection of the splenium of the corpus callosum, pressure on the occipital lobes and interference with circulation in these regions than with the collicular destruction itself.

Case Tdd. Case *Tdd* was trained to figures A4, B4, C4, D4, E4, and F4, including 150–400 overtraining trials per figure in a total of 119 days spread over a period of seven and one-half months. Tantalum wires, gauge 33, were then inserted as shown in Figure 5. The postoperative performance is summarized in Table 3. A4 is the only figure that caused any trouble and this was of questionable significance. *Tdd*'s postoperative record on all the top figures of the test scale is good evidence that dense impregnation of the brain with chemically inert metallic wires does not produce any serious disorganization of pattern perception.

The wires were carefully pulled out of the formalin-fixed brain of *Tdd* and also of *Stf* under a dissecting microscope. In most instances the wires came out cleanly without any adhering layer of tissue. Microscopic examination of the remaining holes (see Fig. 4) showed a wide variation in the degree of scar formation around the wires. In many places there was only a thin film of scar tissue; in others a thick enveloping sheath was present. The thickness of the scar seemed to be correlated with the varying amount of tissue damage caused mechanically by insertion of the wires, being heaviest at points where the damage was

TABLE 3
Postoperative Performance of *Tdd*

Days after operation	14	15	16	17		18	19	20	21	22	23
Negative figures	C4	D4	B4	A4	A3	F4	E4	A4	MS	MS	MS
Errors	0	0	2	3	2	0	2	3	0	1	2
Total trials	20	20	20	8	20	20	20	20	20	20	20

greatest, e.g., where larger blood vessels had been broken.

Cerebellar implants. The entire cerebellum was riddled with implanted tantalum wires in one additional cat otherwise normal. In a second cerebellar case, stainless steel wires were implanted throughout the left half of the cerebellum, while on the right side the wires were inserted and withdrawn in similar locations to equalize the tissue damage on both sides. Functional tests conducted on days 14 through 19 after operation failed to reveal any cerebellar symptoms in either animal.

DISCUSSION

Extensive subpial slicing of the entire visual cortex, or its dense impregnation with metallic wires as described above, failed in either case to produce any marked disturbance of visual pattern perception within the limits of the experimental tests. Good survival of form perception was demonstrated in the ability of the operated animals to discriminate an equilateral triangle from various other triangular figures at a level of performance equal to or closely approaching the preoperative standard.

The absence of a generalized functional breakdown speaks against transcortical intragriseal conduction, including direct current flow, as an important factor in perceptual organization, i.e., in dimensions that might mediate relational effects in form perception.

The stimulus figures were too large to have been projected in most cases into intact cortical tissue between the wires or between the more distantly spaced knife cuts. Furthermore, after operation as well as before, the cats approached the figures more closely—instead of the reverse—when the figures were more difficult. Not uncommonly the operated animals approached the negative figures of all series so closely that the projected retinal patterns must have extended over roughly one-half to two-thirds the entire visual cortex.

The findings in those cases with large bilateral lesions in the tectum discount the possibility that the superior colliculi, or the visual area of the cerebellum to which they relay (9), might have served as substitute centers for the cortical organization. The bordering visual "association" area of the cortex also would seem to be ruled out by the extension of the cuts and the wires into this region.

No abnormalities in visuomotor coordination that could be attributed to the cortical knife cuts or implanted wires were noted at three weeks after operation in casual observations of the cats' ability to jump, to walk a narrow board, or to follow and catch rapidly moving small objects.

It is logically conceivable that, despite perceptual distortions produced by the operations, the positive equilateral triangle may always have appeared less distorted than the negative triangle and been chosen on this basis, or the apparent distortions produced by the operations may have been distinguishable from the actual distortions of the negative figures and were disregarded. These possibilities cannot be rigidly excluded. They are disfavored, however, by the fact that the cats were performing close to the limits of their discriminatory capacity where slight disturbances of any kind tend to cause a breakdown of performance. The distortions caused by the operations ought, theoretically, to have been of such a gross order as to overshadow the lesser actual imperfections that already were reduced to a minimum. Such illusory distortions should frequently have made the positive figure look more distorted than the negative.

The electrical short-circuiting action of metallic conductors inserted in the brain has been discussed at length by Lashley, Chow, and Semmes (5). With or without polarization effects, wires implanted so densely must necessarily have caused considerable distortion in the patterning of any mass "figural" currents. Even in the form of continuously polarized nonconductors, the wires would have destroyed that approximate homogeneity of the cortical tissue that is essential for field theory.

The partial, erratic ensheathing of the wires by scar tissue may have reduced their short-circuiting action. However, if scar tissue has such an effect on current flow, the scars from the subpial knife cuts should themselves have been adequate distorters of field organization.

Since the subpial knife cuts produce a permanent block to ordinary fiber conduction, the results are difficult to reconcile with theories of perception based upon reduplicated interference patterns (4) or upon the alpha rhythm as a scanning device (8). The cuts, involving an erratic invasion of the white matter, should have disrupted any orderly tangential spread of excitations through the gray matter itself or via the short U fibers. The findings seem at present to favor a more vertically organized, motor-conditioned concept of cerebral integration (11).

SUMMARY

To test the importance of transcortical intragriseal conduction in visual pattern perception, the occipital cortex of three cats was subjected to multiple subpial knife cuts intersecting one another in criss-cross patterns and extending through the depth of the gray matter. In four other cases the cortex was densely riddled with tantalum wires inserted in random patterns throughout the visual area and the subjacent white matter. The effects of these operations on perception were tested on a battery of trained form discriminations close to the upper limits of the animals' discriminatory capacity. The general high level of performance after operation indicates that transcortical intragriseal conduction, including direct current flow, is not of critical importance in visual pattern perception.

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